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A FIELD STUDY OF THE LIFE HISTORY OF THE ENDEMIC HAWAIIAN SNAIL *SUCCINEA NEWCOMBIANA*

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Although the Hawaiian land snail fauna is noted worldwide for its diversity and endemism, little is known about the life histories and ecology of most of the endemic Hawaiian species. Hadfield et al. (1993) described the life histories of a few achatinelline tree snail species and, more recently, the life history of a succineid, *Succinea thaanumi*, has been described in laboratory (Rundell & Cowie, 2003) and field studies (Brown et al., 2003a, b). More information on the ecology and life histories of land snail radiations would allow comparisons with other molluscs, such as the freshwater molluscs described by Dillon (2000), and would increase our understanding of allopatric and sympatric speciation (Coyne & Orr, 2004).

In this paper, we report on the life history of *Succinea newcombiana*. In contrast to *S. thaanumi*, which is found on the eastern side of the island of Hawaii from Volcano Village to the Hilo Forest Reserve, *S. newcombiana* is found on the northern side of the island in the Kohala Forest Reserve. The two habitats differ in that *S. thaanumi* is found in rainforests including Puu Makaala, where we previously studied *S. thaanumi*, and which receives a median annual rainfall of 4,000 mm (Giambelluca & Sanderson, 1993), whereas *S. newcombiana* is found in a cloud mist environment where the median annual rainfall is only 2,000 mm (Giambelluca & Sanderson, 1993). Although not as abundant or as widespread as *S. thaanumi*, *S. newcombiana* is relatively common compared to other Hawaiian land snails. The current study was conducted in the Kohala Forest Reserve in a 10 m^2 plot at an elevation of 907 m (20°3.339'N, 155°37.515'W). The understory consisted primarily of an alien torch ginger of the family Zingiberaceae; hapuu, a Hawaiian tree fern (*Cibotium* sp.); and ieie (*Freycinetia* sp.). The overstory consisted primarily of ohia lehua, *Metrosideros polymorpha*, and was less dense than the overstory of Puu Makaala.

Data were collected from 25 January 2003 to 18 January 2004 for a total of 42 observations (1/03 = 1; 2/03 = 2; 3/03 = 2; 4/03 = 2; 5/03 = 3; 6/03 = 6; 7/03 = 4; 8/03 = 5; 9/03 = 4; 10/03 = 4; 11/03 = 5; 12/03 = 3; 1/04 = 1). More observations were made during the summer months because we were following egg masses. All plants, up to 1.8 m high, in the study area were examined for the presence of snails and egg masses by at least two observers during each observation. Maximum shell length of all snails was measured with a ruler *in situ* with a minimum amount of contact. Additionally, we recorded snail activity. In the past, we recorded activity based on whether a snail was extended out of its shell (Brown et al., 2003a). However, because *S. newcombiana* could not completely retract their bodies into their shells, we based activity on whether or not the snail's eye stalks were retracted. We recorded the snail's placement on a plant: top or bottom of a leaf, petiole, flower or stem. Only a few snails were observed on the petioles, flowers or stems of the plants, so we did not include these data in the behavioral analyses. Number of egg masses found and the number of embryos in each mass were recorded. Temperature and humidity data were gathered during each observation period with a RadioShack temperature/humidity gauge.

To examine the relationship between behavior and the microclimate variables across the 42 observations, we computed simple correlations between the total number of observed snails, the number of snails found on the top of a leaf with their eye stalks in, the number of snails found on the top of a leaf with their eye stalks out, the number of snails found on the bottom of a leaf with their eye stalks in, the number of snails on the bottom of a leaf with their eye stalks out, the total number of snails with their eye stalks out regardless of their location on a plant, and the microclimate variables of temperature and humidity.

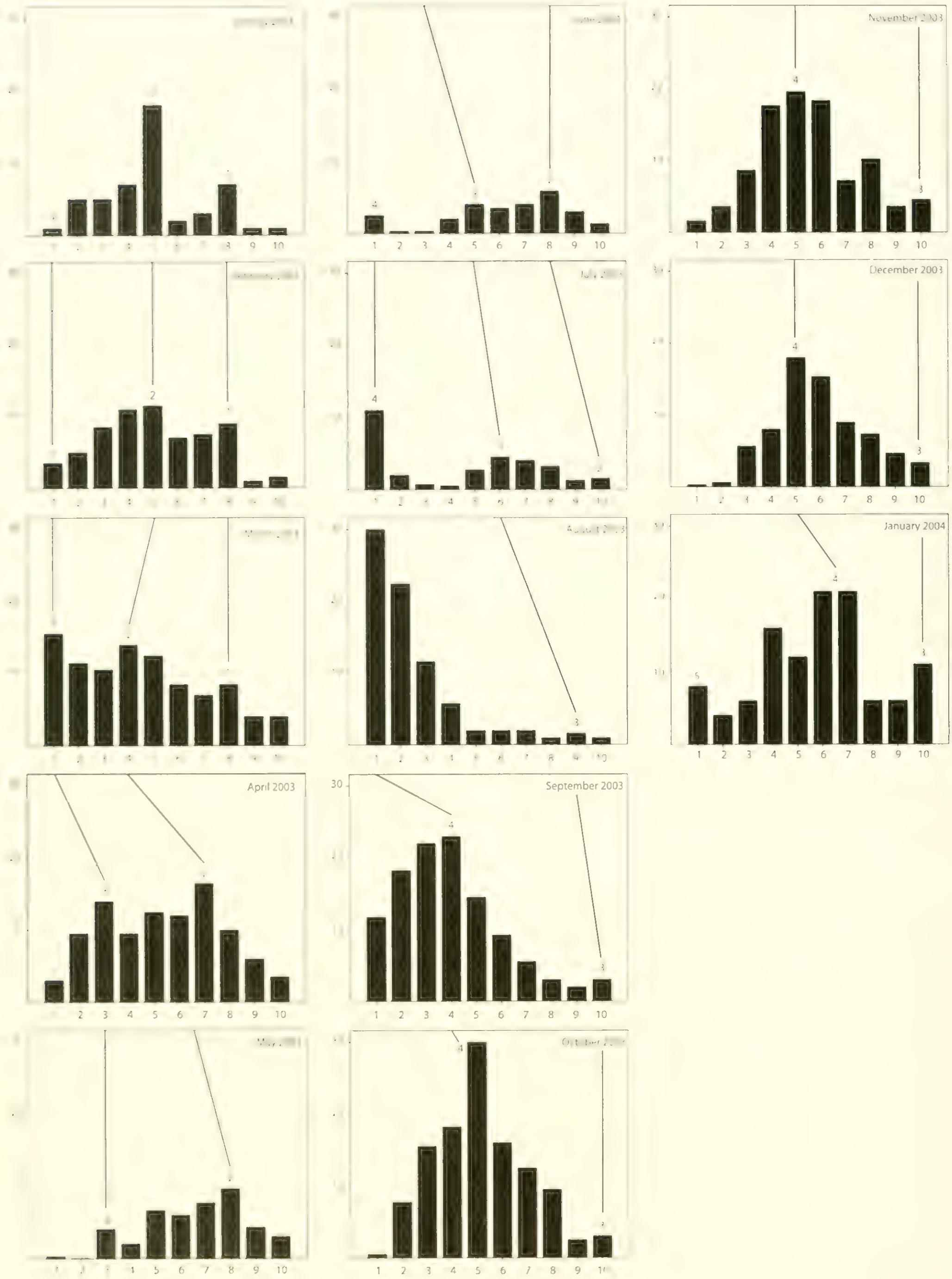

FIG. 1. Monthly frequency distributions of snail size. The Y-axis is the average number of snails of a particular size observed across a month (Number of observations per month: 1/03 = 1; 2/03 = 2; 3/03 = 2; 4/03 = 2; 5/03 = 3; 6/03 = 6; 7/03 = 4; 8/03 = 5; 9/03 = 4; 10/03 = 4; 11/03 = 5; 12/03 = 3; 1/04 = 1). The X-axis is snail shell size in mm. In August 2003, there were 52 snails 1 mm in size rather than 30.

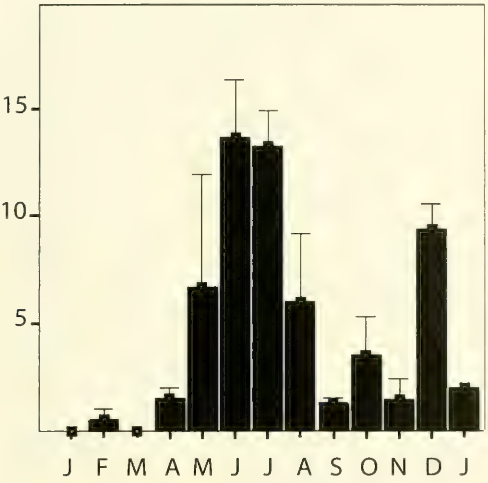

FIG. 2. Frequency distribution of the mean number of egg masses observed across a month. The letters on the X-axis are the first letters of a month beginning with January. Bars represent the standard errors of the mean.

The snails and their egg masses were found primarily on the alien ginger plants. Snail sizes varied across the year and showed two distinct lineages (Fig. 1). In January 2003, there were three cohorts of snails: cohort 1 contained adult snails, cohort 2 contained half-grown snails, and cohort 3 contained newly emerged snails. As the months proceeded, the adult snails in cohort 1 disappeared. Snails in cohort 2 grew from January through July, laid eggs in June and July (Fig. 2) and disappeared in August. Snails in cohort 3 emerged from their eggs masses from January through March, grew from March through August, laid eggs in December (Fig. 2), and formed a cohort of adult snails in January 2004 similar to cohort 1 observed in January 2003. From July through September, snails emerged from egg masses laid by cohort 2 and became cohort 4. Cohort 4 snails grew from August to January 2004 and formed a cohort of half-grown snails similar to cohort 2 observed in January 2003. Finally, cohort 5 consisted of snails emerging from egg masses laid by cohort 3 in December and was similar to cohort 3 observed in January 2003 (Fig. 1). Therefore, we observed two lineages: lineage 1 was formed from cohorts 1, 3 and 5; lineage 2 from cohorts 2 and 4.

Egg masses were translucent like those of *S. thaanumi* (Brown et al., 2003b). The number of new egg masses declined from August through November but increased dramatically in December (Fig. 2), followed by a second decrease in January 2004. Although many fewer egg masses were laid in December (n = 28) than from May to August (n = 185), the December egg masses contained significantly more embryos (Fig. 3) than the May to August masses ($X^2_{(3)} = 22.16$; $p < 0.0001$).

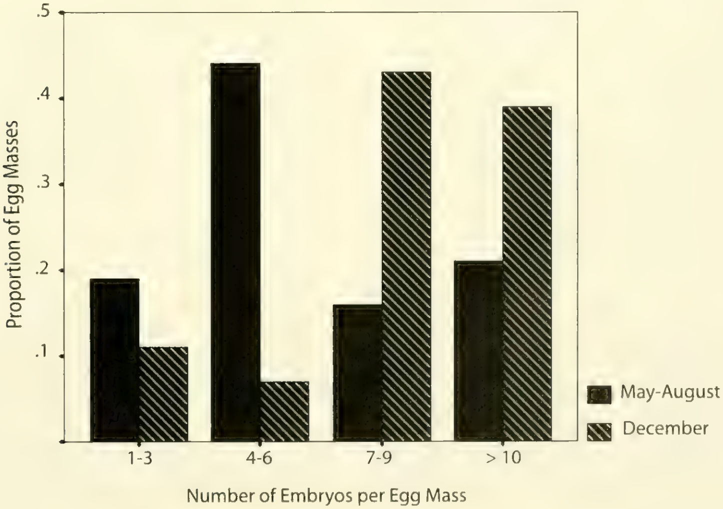

FIG. 3. Bar graph of the number of embryos in a clutch of eggs during the two major laying seasons.

We interpreted the above growth patterns for *S. newcombiana* as indicating an annual, semelparous life cycle for two snail lineages. Most snails probably lived about 12 months. These life cycles were similar to the life cycle of *S. thaanumi* (Brown et al., 2003a), but the data on *S. thaanumi* reflected a single snail lineage. The egg masses of the two lineages of snails also differed. Snails in cohort 2 laid more egg masses with fewer embryos, whereas snails in cohort 3 laid fewer eggs masses with more embryos per mass. At present, we do not know if the two lineages have different haplotypes.

Mating was observed five times during the study: 2/1/03, 5/22/03, 6/16/03, 6/30/03, and 7/7/03. As we found with *S. thaanumi* (Brown et al., 2003a), the smaller snail acted as the male (succineids are hermaphrodites), but, unlike *S. thaanumi*, we observed mating only between dyads (no triads as we previously observed with *S. thaanumi*).

Snail behavior was related to the microclimates of the study area. Snails were more likely to be found on the bottom of a leaf with their eyes stalks in when temperature was higher ($r = 0.66$; $p < 0.01$; $N = 42$ for all correlations) and humidity was lower ($r = -0.72$; $p < 0.01$). Snails found on the tops of leaves were also more likely to have their eye stalks in when temperature was higher ($r = 0.49$; $p < 0.01$) and humidity was lower ($r = -0.50$; $p < 0.01$). Snails with their eye stalks out that were active on the plants, however, were found at all temperatures ($r = -0.03$) and humidities ($r = 0.07$). This differed noticeably from our observations of *S. thaanumi*. In high temperature and low humidity conditions, we seldom observed active *S. thaanumi*, but we often observed active *S. newcombiana* in direct sunlight and low humidity conditions. The total number of snails observed was also not related to temperature ($r = 0.18$) or humidity ($r = -0.16$). Again, this differed from our previous observations of *S. thaanumi*, for which we observed fewer snails as the temperature increased, suggesting that the snails moved to a different part of their habitat. *Succinea newcombiana* cannot retract into its shell, whereas *S. thaanumi* can do so. Because of its inability to retract into its shell, one might conclude that *S. newcombiana* is more susceptible to high temperature and low humidity than *S. thaanumi*, but this was not the case. These behavioral differences to high temperature and low humidity might be related to the different ecotypes the two species occupy. The population *S. newcombiana* is found in a cloud mist forest with relatively less rainfall but more mist, whereas populations of *S. thaanumi* are found in rainforest habitat with relatively more rainfall and less mist. *Succinea newcombiana* might have lost the ability to retract into its shell because of the presence of abundant moisture in the air.

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